Pollen morphology and Plant taxonomy. *VIII.* Didiereaceae.

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Abstract.

Didiereaceae has several features in common with certain centrospermous plants [floral details, dioecism included; arboreal or semiarboreal habit, presence of spines, absence of stipules, etc.; cf. particularly *Nyctaginiaceae* (*Phaeoptilum* etc.)]. The evidence of pollen morphology, particularly that derived from the study of sporoderm stratification, favours the idea of referring *Didiereaceae* to *Centrospermae*.

Terminology.

The term « sporoderm » (sporodermis), as suggested by Leitgeb (1883) and others, means the wall, all layers included, of pollen grains and spores. In cormophyte sporoderms the different layers, from the inside outwards, may be classified as follows :

A. Soft (malacodermic) layers (as a rule not preserved in fossil pollen grains or spores) : Intine (endosporium).

B. Entirely or chiefly hard (sclerodermic) layers (Sclerine), as a rule preserved in fossil pollen grains and spores.

I. Exine (exosporium).

a. Nonsculptured exine : Nexine.

1. Endonexine : the innermost, strongly refractive, usually very thin nexine layer.

(2. Mesonexine : of local occurrence, forming thickenings at apertures, etc.).

3. Ectonexine : the outer, thicker, less refractive nexine layer.

b. The sculptured part of the exine : Sexine. Among planerogams the basic structure of the sexine seems to be small drumstick-shaped rods (pila), projecting at right angles from the outer surface of the nexine. A pilum consists of a head (caput) and a rodlike pars collaris, or baculum. In baculate exines the heads of the pila coalesce laterally.

II. Perine (perisporium). A perine is formed when a medium with perigeneous properties is present at the formation of the spore wall. It is sometimes difficult to decide whether a certain stratum or sculptural element is perinous or exinous. In such cases « Sculptine » may be used as a provisional, neutral term, embracing any strata, or fragments of strata, belonging to the exine (n. b., the sexine), the perine, or to both.

For explanation of terms relating to apertures, size, and shape of the pollen grains, see ERDTMAN 1943 and 1944-46.

KEY TO THE SPECIES.

The pollen grains in *Didiereaceae* are 4 — 7 -colpate, large (length of longest diameter usually between 50 and 100 μ), spherical to suboblate, less frequently subprolate. The exine consists of a well developed sexine and a less prominent nexine. The sexine is more or less distinctly baculate and provided with small perforations (cf. fig. : 1, 4-5) leading from the outside to the interstices between the bacula. The contour line of the pollen grains is slightly rough owing to the presence of minute spinules.

Two colpae are occasionally seen to unite near one of the poles. As to the size of the colpae and other details not mentioned in the text, reference is made to the illustrations.

A. Colpae clearly delimited, with rounded ends ; sexine baculate, although not very distinctly.
  I. Spinules not vestigial ; nexine thickness 2.25 μ or less.. *Alluaudia.*
    a. Maximum diameter < 70 μ.
      1. Spinules about 0.5 μ..... *A. procera.*
      2. Spinules about 1.00 — 1.25 μ.
        α. Exine thickness about 4.5 μ..... *A. comosa.*
        β. Exine thickness about 5.75 μ..... *A. Humberti.*
    b. Maximum diameter > 70 μ.
      1. Nexine thickness about 1.25 μ..... *A. ascendens.*
      2. Nexine thickness about 1.75 — 2.25 μ.
        α. Spinules 1.25 μ ; grains 5 — 7- colpate..... *A. Humberti.*
        β. Spinules 1.75 μ ; grains 7-colpate..... *A. dumosa.*
  II. Spinules vestigial (or sometimes even absent ?) ; nexine thickness about 2.75 μ..... *Alluaudiopsis.*

B. Colpae not sharply defined ; sexine distinctly baculate.
  I. Maximum diameter (57 —) 65 (— 72) μ ; exine thickness about 3.5 μ..... *Decaryia.*
  II. Maximum diameter (65 —) 70 (— 78) μ ; exine thickness about 3.25 μ..... *Didierea.*

DIAGNOSES.

Alluaudia ascendens DRAKE (HUMBERT n. 5701).

Pollen grains (5-) 6 — 7 -colpate, large (71 — *85* — 99 μ ; 71 is the minimum, *85* the average, and 99 the maximum length of the longest diameter, spinules not included, of ten acetolyzed pollen grains from herbarium specimens ; when expressing the average size of large pollen grains, such as in this and the following species, approximations may be made according to the following examples : 78 — 82 μ to be quoted as 80 μ, and 83 — 87 as 85 μ, etc.). Exine

thickness at the equator (halfway between two colpae of grains subjected to acetolysis and chlorination) about 6.5 μ (nexine 1.25, sexine 5.25). Length of spinules about 1.5 μ. (The thickness of the sporoderm layers and the length of the spinules were measured on camera lucida drawings, × 1600).

In addition to the colpae one or two poroid arcas have occasionally been observed in the pollen grains of this species.

Alluaudia comosa Drake (Alluaud n. 114).

Pollen grains 6 — 7 -colpate, large (48 — *55* — 61 μ) ; exine thickness about 4.5 μ (nexine 1.5, sexine 3.0). Spinules densely spaced, about 1.00 — 1.25 μ in length.

Alluaudia dumosa Drake (Humbert n. 20313).

Pollen grains 7 -colpate, large (75 — *80* — 100 μ), usually oblate spheroidal [polar axis : equatorial diameter = (0.85 —) 0.90 (— 1.06)]. Exine thickness about 8.75 μ [nexine 2.25 (endonexine 0.75, ectonexine 1.50), sexine 6.50] ; spinules about 1.5 μ.

In addition to the colpae one or two poroid areas have occasionally been observed in the pollen grains of this species.

Alluauadia Humberti Choux (Humbert n. 11593).

Pollen grains 5 — 6 (— 7) -colpate, large (55 — *65* — 75 μ). Exine thickness about 5.75 μ (nexine 1.75, sexine 4.00) ; spinules about 1.25 μ.

Alluaudia procera Drake (Decary n. 9255 ; Perrier de la Bâthie n. 17644).

Pollen grains (5 —) 6 -colpate, generally large (45 — *55* — 65 μ). Exine thickness about 3.5 μ (nexinc 1.0, sexine 2.5) ; spinulcs about 0.3 — 0.5 μ.

Alluaudiopsis fiherenensis Humb. et Choux (Humbert n. 11588).

Pollen grains 4 — 5 -colpate, large, exceptionally very large (78 — *85* — 108 μ). Exine thickness about 8.5 μ (nexine 2.75, sexine 5.75) ; spinules 0.0 — 0.6 μ.

Decaryia madagascariensis Choux (Humbert n. 20318).

Pollen grains 5 — 6 -colpate, large (57 — *65* — 72 μ), suboblate (0.85) to subprolate (1.30). Exine thickness about 3.5 μ [nexine 1.25, sexine 2.25 (bacula 1.50)] ; spinules about 1.00 — 1.25 μ.

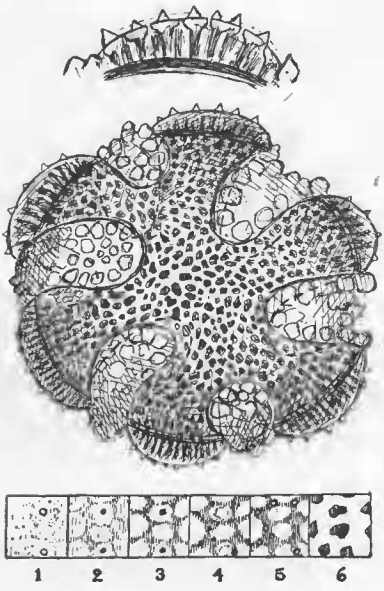
Didierea madagascariensis H. Bn (Decary n. 3352).

Pollen grains 6-colpate, large (65 — *70* — 78 μ). Exine thickness about 3.25 μ [nexine 1.00 (endonexine one third, extonexine two

thirds), sexine 2.25 (bacula 1.50)] ; spinules about 1.0 — 1.5 μ.

As shown by the above key most species of the family can be separated by sclerinc characteristics only. Close agreement, however, exists between the pollen grains of *Decaryia* and those of *Didierea*.

Figures from the diagnoses are collocated in tab. 1, p. 372.



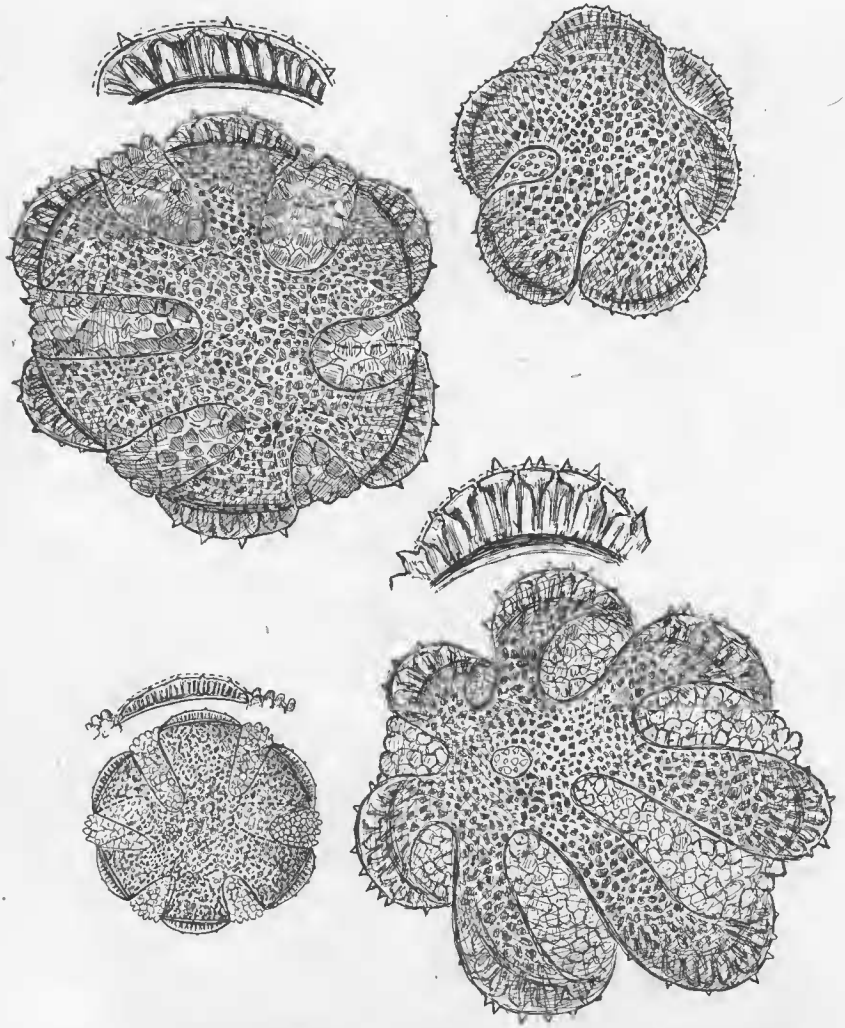
Pl. 1. — Pollen grain of *Alluaudia Humberti* Choux. Polar view, × 625 (1 cm. represents 16 μ). Upper detail figure (× 1250) : sporoderm stratification in optical section, exhibiting conical spinules, a line of refraction (the broken thin line), sexine perforations, bacula, etc. Lower detail figure : details of sporoderm stratification in surface view at different adjustments of the microscope from high (1) to low (6). I : two spines, gradually disappearing in 2-4.4 : sexine perforations (disappearing in 5). 6 : lower part of bacula (irregular-polygonal, in optical section).

Palynotaxonomy.

Particularly after the impetus given by Wodehouse (1935) pollen morphology is being used to a greater extent as an aid in plant taxonomy. Usually only the gross features of the pollen grains — the apertures, and the size and shape of the grains — are considered. Even the sum of their evidence may however, and this seems to be the case in *Didiereaceae*, fail to affect the needle of the taxonomical compass. In such cases it should be supplemented by a study of sporoderm stratigraphy and sculpture.

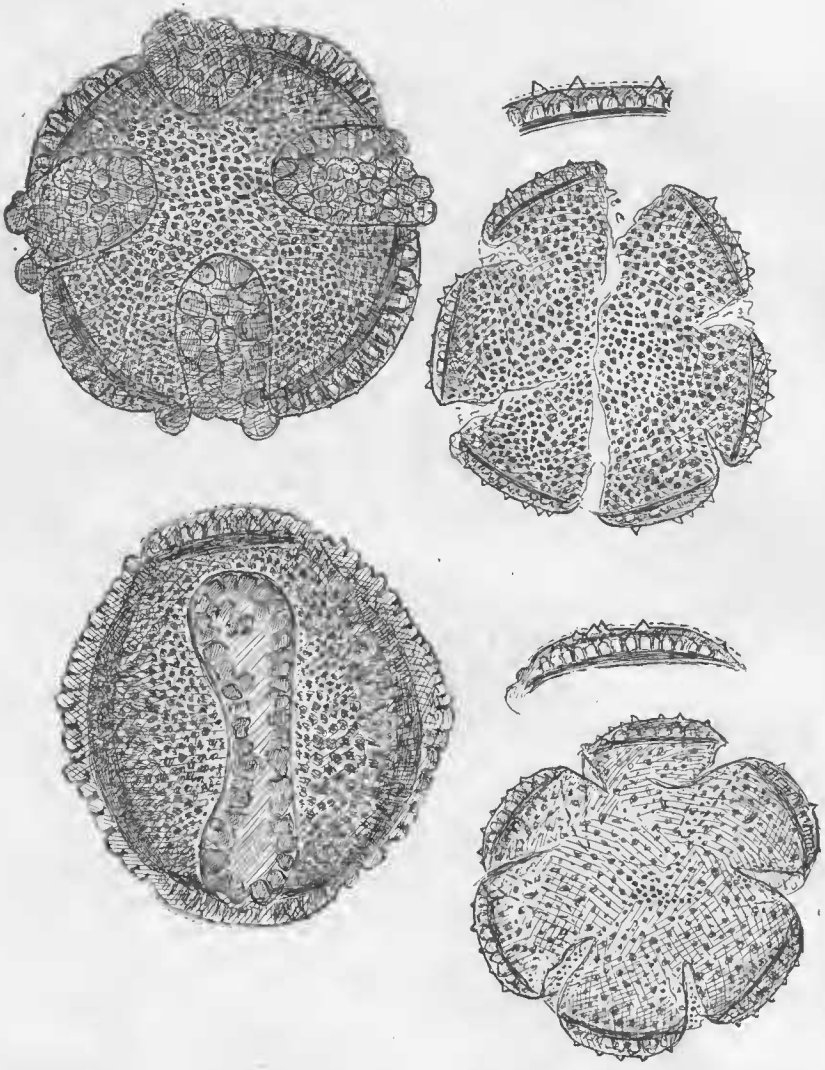
In dealing with *Didiereaceae* we may e.g. ask whether pollen

grains with the combination spinules — sexine perforations — bacula occur also in other families. A definite answer to this question cannot yet be given, but pollen grains with the above combination do occur in a few sympetalous families, viz. *Convolvulaceae* (*Calystegia*) and *Polemoniaceae* (*Loeselia*). Furthermore they are often



Pl. II. — Pollen grains in *Didiereaceae* × 625 (1 cm. represents 16 μ). Upper detail, left : *Alluaudia ascendens* Drake (polar view). — Upper detail, right : *A. comosa* Drake (polar view). — Lower detail, left : *A. procera* Drake (polar view). — Lower detail, right : *A. dumosa* Drake (oblique view).

found in plants belonging to the *Centrospermae* (*Aizoaceae* : *Mesembryanthemum conspicuum*; *Amaranthaceae*: *Trichinium*; *Basellaceae*: *Boussingaultia*, *Ullucus*; *Caryophyllaceae* : *Agrostemma*, *Saponaria*,



Pl. III. — Pollen grains in *Didiereaceae* × 625 (1 cm. represents 16 μ) Upper detail, left: *Alluaudiopsis fiherenensis* Humb. et Choux (polar view). — Lower detail, left : *A. fiherenensis* (equatorial view). — Upper detail, right : *Didierea madagascariensis* H. Bn. (polar view). — Lower detail, right : *Decaryia madagascariensis* Choux (polar view).

Scleranthus ; *Nyctaginiaceae* : *Allionia, Boerhavia, Mirabilis, Phaeoptilum, Rockia* ; *Portulacaceae* : *Calandrinia, Claytonia, Lewisia, Montia, Portulaca, Spraguea*) and *Opuntiales* (*Cereus, Echinopsis, Peireskia, Phyllocactus, Rebutia, Selenicereus, Trichocereus*, etc.).

Tab. 1. Apertures, size, and sporoderm stratification in the pollen grains of *Didiereaceae*.

	Apertures (number of colpae)	size (μ)			sporoderm stratification (sclerine only)			
		max. diameter			exine thickness (μ)			length of spinules (μ)
		min.	appr. average	max.	nexine	sexine	total	
Alluaudia ascendens.....	(5) 6-7	71	85	99	1.25	5.25	6.50	1.5
A. comosa.....	6-7	48	55	61	1.50	3.00	4.50	1.00-1.25
A. dumosa.....	7	75	80	100	2.25	6.50	8.75	1.5
A. Humberti....	5-6 (7)	55	65	75	1.75	4.00	5.75	1.25
A. procera.....	(5-)6	45	55	65	1.00	2.50	3.50	0.3-0.5
Alluaudiopsis ...	4-5	78	85	108	2.75	5.75	8.50	0.0-0.6
Decaryia	5-6	57	65	72	1.25	2.25	3.50	1.00-1.25
Didierea.....	6	65	70	78	1.00	2.25	3.25	1.00-1.50

Perforate baculate exines without spinules (as found in a part of the pollen grains of *Alluaudiopsis*) have likewise been encountered in some members of the *Centrospermae* (e. g. *Phytolacca* and *Pteranthus*) and *Opuntiales* (*Echinocactus, Mamillaria, Nopalea*). They also occur in *Simmondsia californica* Nutt., a shrub usually regarded as a member of *Buxaceae* but referred by van Tieghem (1898) to a family of its own near *Aizoaceae*.

The evidence of sporoderm stratigraphy thus seems to support the idea of Radlkofer (1896), who referred *Didierea* to a family of its own, which was tentatively placed in the *Centrospermae*. Among these particularly *Nyctaginiaceae* (cf. e.g. *Phaeoptilum*) exhibits several features in common with *Didiereaceae* [cf. e.g. floral morphology (including dioecism), arboreal or semi-arboreal habit, presence of spines, absence of stipules, etc.].

The reasons of referring *Didiereaceae* to *Sapindales*, as suggested by Choux (1934), Drake del Castillo (1903), Engler and Diels (1936), Hutchinson (1926), and Perrot and Guérin (1903), are admittedly vague and not supported by the evidence of pollen morphology although rods and spinules, more or less similar to those in *Didiereaceae*, do occur in certain members of *Buxaceae* and

Icacinaceae as well as in *Xanthoceras sorbifolia* (*Sapindaceae*). The combination spinules — sexine perforations — bacula has not, however, been found in *Sapindales* sensu Engler and Diels.

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